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HADROSAURIAN DINOSAUR BILLS—MORPHOLOGY AND FUNCTION

By WILLIAM J. MORRIS

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HADROSAURIAN DINOSAUR BILLS—MORPHOLOGY AND FUNCTION

By William J. Morris[1]

Abstract: Reconsideration of the morphology and function of the bill of hadrosaurian dinosaurs is based upon an excellently preserved bill mold of a recently discovered specimen (LACM 23502) assigned to the genus *Anatosaurus*. Morphology suggests a filtering function for the bill and adaptation for discharge of fluid and small particles following intake and mastication of plant or invertebrate food.

Acknowledgments

The excellent specimen of *Anatosaurus cf. annectens* (LACM 23502) upon which this study is based was discovered and collected by H. Garbani and skillfully prepared by M. Odano, both of the Los Angeles County Museum of Natural History. The skeleton was found in the Hell Creek Formation south of Ft. Peck Reservoir, NE ¼, Sec. 36, T21N, R35E, Montana.

The project, leading to this discovery as well as other important dinosaur finds, was generously supported by Mr. and Mrs. William T. Sesnon, Jr., patrons of the Los Angeles County Museum of Natural History.

Constructive criticism of the manuscript by Dale Russell, Canadian National Museum, and Theodore Downs of the Los Angeles County Museum of Natural History is appreciated. Others on the staff of the Los Angeles County Museum whose help is acknowledged are: David Forstch and Alan Tabrum for their interest and discussion, and Joseph Cocke for his drawing of Figure 2. The remainder of the illustrations and photographs were done by the author.

Introduction

Dinosaurs of the family Hadrosauridae are among the most familiar Late Cretaceous fossils. Indeed, the first dinosaurs described from North America, belonged to these so called duckbilled forms. Prior to a brief description by Cope (1883) the presence of a horny bill in hadrosaurs was conjectural. Cope, in preparing a specimen of *Anatosaurus annectens*, discovered portions of a mold of the bill. Later two other specimens in which most of the bill was preserved were described for *A. annectens* by Versluys (1923) and for *Corythosaurus excavatus* by Sternberg (1935). In all three cases we must rely upon the description of the bill as the original molds were either destroyed during preparation or subsequently lost. As a result, a recently discovered specimen of *Anatosaurs cf. annectens* (LACM 23502) from the Hell Creek beds of Montana containing a well preserved mold is most important in

[1]Research Associate in Vertebrate Paleontology, Los Angeles County Museum of Natural History; and Professor of Geology, Occidental College, Los Angeles, California 90041.

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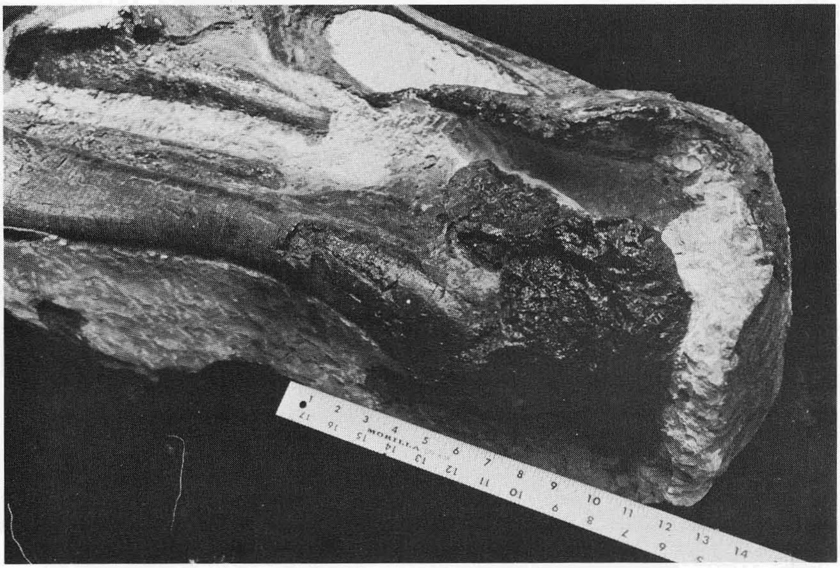

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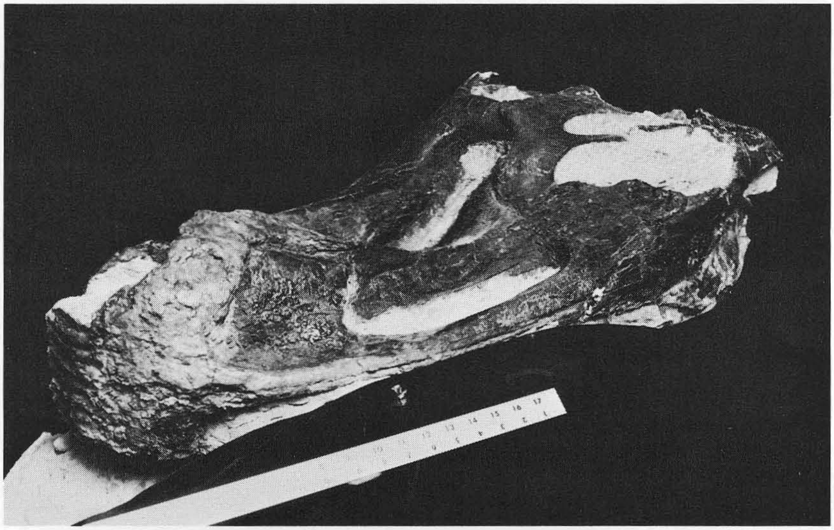

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evaluating the morphology and function of the hadrosaurian bill. The letter designations are used to designate specimens in various museums: LACM, Los Angeles County Museum of Natural History; ROM, Royal Ontario Museum; NMC, National Museum of Natural Sciences, Ottawa.

BILL MORPHOLOGY OF ANATOSAURUS CF. *A. ANNECTENS* (LACM 23502)

The specimen is a mature individual approximately forty feet long. The skull is only slightly distorted mainly along a parasagittal section approximately midway between the orbits and narial openings. The mandibles, though offset to the right, are not distorted relative to the midline so that the bill mold is undistorted, (Fig. 1). Morphologically, the specimen is very similar to *A. annectens* but there are some differences between it and the holotype. Until the time when careful study has been made regarding individual variability of hadrosaurian dinosaurs, it is hazardous to make positive, specific references for specimens other than the type. This is especially true regarding the LACM specimen for it was found further north than the Lance Formation, Wyoming, localities from which the types of *A. annectens* were obtained.

The bill mold is composed of gray, lithic siltstone, the surface is accentuated by a thin veneer of iron oxide. In the figures, the mold appears dark due to the application of preservative although it has the same composition as the matrix. The entire anterior surface (attached dorsally to the premaxillary region) is preserved and only a small portion of the ventral edge is lacking. Only the left side is preserved.

Before discussing the form and function of the bill it is important to describe the geometry of the mold. Errors in interpretation by other authors seems largely to have resulted from misinterpretation of the geometry of the mold.

When the specimen was discovered, anterior and posterior sides of the mold were preserved with a very thin surface of weakness separating them. The surface, shown in Figures 1, A, B, C and D, is the posterior side of the mold, the one closest to the premaxillary region of the skull. It is important to note that matrix on both sides of the preserved surface was carefully prepared and other structures were not found within the matrix except the surface of the mold. Hence the entire bill, as preserved, is represented by two surfaces separated by less than 0.01 mm, one of which is shown in the figures.

The surface of the mold is vertically fluted, containing nine or possibly ten V-shaped channels. These are separated by dorsal-ventral pillars, rounded

Figure 1. Partially prepared skull of *Anatosaurus* cf. *annectens*, LACM 23502. (A) Complete skull, left side. The bill mold is not preserved on this side but the edge of the mold can be seen extending ventrally from the premaxillary below the predentary of the lower mandible. Note that the free margin of the mold extends below the predentary and is separated from the predentary by siltstone matrix. (B) Anterior undulating surface of the bill mold showing the fluted channels preserved as an iron oxide veneer on the siltstone matrix. (C) Dorsal oblique aspect of the skull illustrating the very terminal position of the bill mold along the ventral margin of the premaxillary. (D) Ventral oblique view showing the bill mold and the matrix layer separating it from the predentary.

in cross section. Laterally, towards the maxillaries, the fluted surface is replaced by a smooth triangular plate.

The mold is approximately 110 mm long at the junction of the premaxillaries and it extends ventrally about 50 mm below the anterior margin of the predentary, decidedly overlapping the front of the lower jaw. Although the extreme ventral margin of the mold appears to be missing, the taper of the pillars and channels suggests that the entire bill was not much longer than shown in this specimen.

The premaxillary of the specimen, dorsal to the mold on the left side, is not well preserved and the surface separating bill and upper jaw cannot be seen. There is, however, little doubt that the bill was united with the upper mandible. A complimentary structure that would have been attached to the lower mandible was not found even though conditions for its preservation must have been similar to those for the upper bill mold.

INTERPRETIVE MORPHOLOGY

The surface of the mold forms an immediate extension of the premaxillary without break or offset. The actual horny bill must have been affixed anterior to the mold and, in order to be secure, must have extended up and onto the surface of the premaxillaries. Although there is no direct evidence indicating the posterior limit of the bill, it probably did not extend farther than the excavation surrounding the nares in the premaxillaries.

The geometry suggested by the anterior position of the mold suggests that the mold reflects the interior surface of the bill. Probably some compression of the bill occurred during compaction of the silt now forming the matrix, and

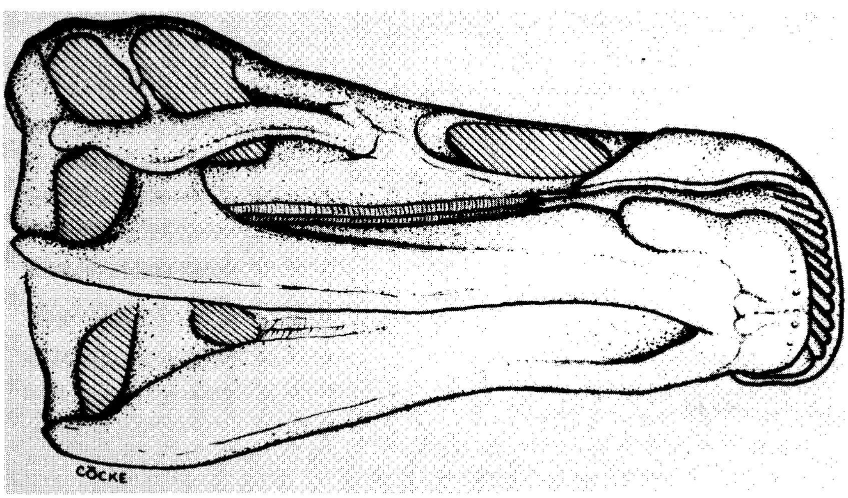

Figure 2. Restoration of the bill on the skull of *Anatosaurus* cf. *annectens*, LACM 23502. The undulating, fluted inner surface of the bill is shown. When the mandibles were closed and the predentary opposed to the bill, channels opening from the mouth were formed.

it is impossible to determine the original thickness of the specimen. The fluted surface was evidently confined to the interior of the bill as no comparable surface was found against the more dorsal surfaces of the premaxillary. Conceivably the original exterior fluting could have been destroyed during compaction but then why was it not also destroyed on the more ventral portion? It seems best to reconstruct a bill with the fluted surface only on the internal side.

The predentary is poorly preserved and furnishes no evidence for a bill on the lower jaw. Nor was evidence for the presence of a lower bill found in the matrix anterior to the predentary.

A restoration of the probable appearance of the upper bill is shown in Figure 5.

DISCUSSION OF PREVIOUSLY DESCRIBED BILL MOLDS

The specimen described by Cope was destroyed during preparation of the skull. Cope did not give a reason for destroying the mold, but one cannot help conjecturing that he thought his description vivid enough that future reference to the specimen would be unnecessary. The mold of the *Corythosaurus excavatus* specimen, except for a very small and unilluminating fragment, could not be located. In the third example Versluys apparently used the mold to cast what he took to be a plaster replica of the bill and, after obtaining the cast, the natural mold was not retained.

Cope appears to have misinterpreted a structure very similar to that of LACM 23502. The full text follows (1883:106): "Dermal or corneous structures have left distinct traces in the soft matrix about the end of the beak-like muzzle. Laminae of brown remnants of organic structures were exposed in removing the matrix. One of these extends as a broad vertical band round the sides, indicating a vertical rim to the lower jaw, like that which surrounds some tea trays, and which probably represents the tomia of the horny sheath of a bird's beak. At the front of the muzzle its face is sharply undulate, presenting the appearance of vertical columns with tooth-like apices. Corresponding tooth-like processes, of much smaller size, alternate with them from the upper jaw. These probably are the remains of a serration of the extremital part of the horny tomia, such as exists on the lateral portions in the lamellirostral birds."

Cope described an undulatory surface with tooth like terminations; however, he did not make it clear whether he considered the object examined a mold or the actual bill. He implies that the structure was attached to the lower jaw and that only small protuberances were present on the upper. Cope probably misinterpreted the area for attachment of the bill, judging from the LACM specimen. Versluys (1923) also believed that Cope's analysis was in error, but Lull and Wright (1942) and Ostrom (1961) both accepted Cope's (1883) description of a horny beak on the lower jaw. Probably the smaller, tooth like processes described by Cope were rugosities normally present distally on most hadrosaurian premaxillaries.

The morphology of the hadrosaurian bill was further confused by Lull and Wright who state (1942:43), "In the Senckenberg specimen [the one

described by Versluys] the impression shows a beak on the upper jaw which projected with a free lower border for about 8 cm over the ventral edge of the premaxillae. The beak stood vertically, with a regular, undulating surface which became smoother towards the sides. Cope described the same wavy appearance corresponding and alternating with the tooth-like processes in the jaw itself. . . . He [Cope] also described a similar horny beak on the lower jaw."

Cope of course had not described a wavy appearing structure occurring on both jaws, the upper being described as small tooth like processes. Ostrom (1961:152) apparently agreed with Lull and Wright stating, "Cope (1883), however, described beak impressions at the anterior extremities of both the upper and lower jaws in a specimen of *A. copei* (*Diclonius mirabilis*)." Yet neither LACM 23502 nor the equally well preserved Senckenberg specimen give any indication of a lower bill.

Sternberg figured a bill mold in describing a specimen of *C. excavatus* (NMC 8676), but in neither the plate explanation nor in the body of the paper did he state that the bill was attached to the lower mandible (Fig. 3). Ostrom, however, (1961:152) states, "Further evidence of a lower beak has been found in a third specimen (*Corythosaurus excavatus*), (NMC 8676), described by Charles M. Sternberg (1935), in the form of an impression of an incomplete horny beak in front of and along the left side of the predentary." As the plate from Sternberg's paper shows (Fig. 3) the mold is a fluted surface associated with the lower jaw but it is separated from the predentary by a considerable thickness of rock matrix. The presence of matrix between the surface and predentary is evidence that the mold is not the opposing surface of a predentary sheath. Upon examination of the plate and the small fragment in the collection of the Canadian National Museum, it appears as though the mold is that portion of the upper bill which originally projected over and in front of the predentary.

Although the fluted surface has been observed on three reported species, there is a problem regarding it. Does the fluted surface belong on the external surface or the internal surface of the bill?

Cope, (1883) having interpreted the mold as being attached to the lower jaw, apparently assigned the undulatory surface to the exterior of the lower bill. On the other hand, Versluys (1923) assigned the undulatory surface to the outer surface of the upper bill. Versluys presents excellent drawings showing that the bill was indeed attached to the upper mandible and that the feature is similar to the mold in LACM 23502. However, in reconstructing the bill he placed the undulatory surface on the exterior. Versluys removed the posterior portion of the bill mold and then poured a substance, probably plaster, against the anterior part of the mold, judging from the wording as translated from German. The resulting cast was retained but the rest of the mold was not. Versluys interpreted this cast as being the bill. He had apparently reproduced the posterior part of the original mold formerly occupied by matrix. Such a restoration would erroneously cause the undulatory surface to appear on the exterior rather than on the interior of the bill.

Sternberg (1935) did not state whether he believed the undulatory surface

of the beak to be on the exterior or the interior. Ostrom, however, in discussing the specimen of *Corythosaurus excavatus* described by Sternberg, states, (1961:152), "This specimen indicates the presence of small, tooth-like projections on the inner surface of the beak, which probably contributed to a firm union of this structure with the lower jaw." Sternberg's plate clearly shows a layer of matrix between the mold and predentary which is evidence against a firm union. In addition, the surface of the predentary, although rugose, is not appressed against the mold of the bill and the rugosities do not match the channels in the bill mold.

The various interpretations of the relationship of the undulatory surface to the mandibles is illustrated in Figure 4.

FUNCTION OF THE HADROSAURIAN BILL

Almost every conceivable mode of food gathering has been proposed at one time or another for the hadrosaurian dinosaurs. There are no existing

Figure 3. Lower jaw of *Corythosaurus excavatus*, NMC 8676, showing the bill mold (H.B.), predentary (P.D.), and dentary (D). This figure is reproduced from Plate II, Sternberg (3).

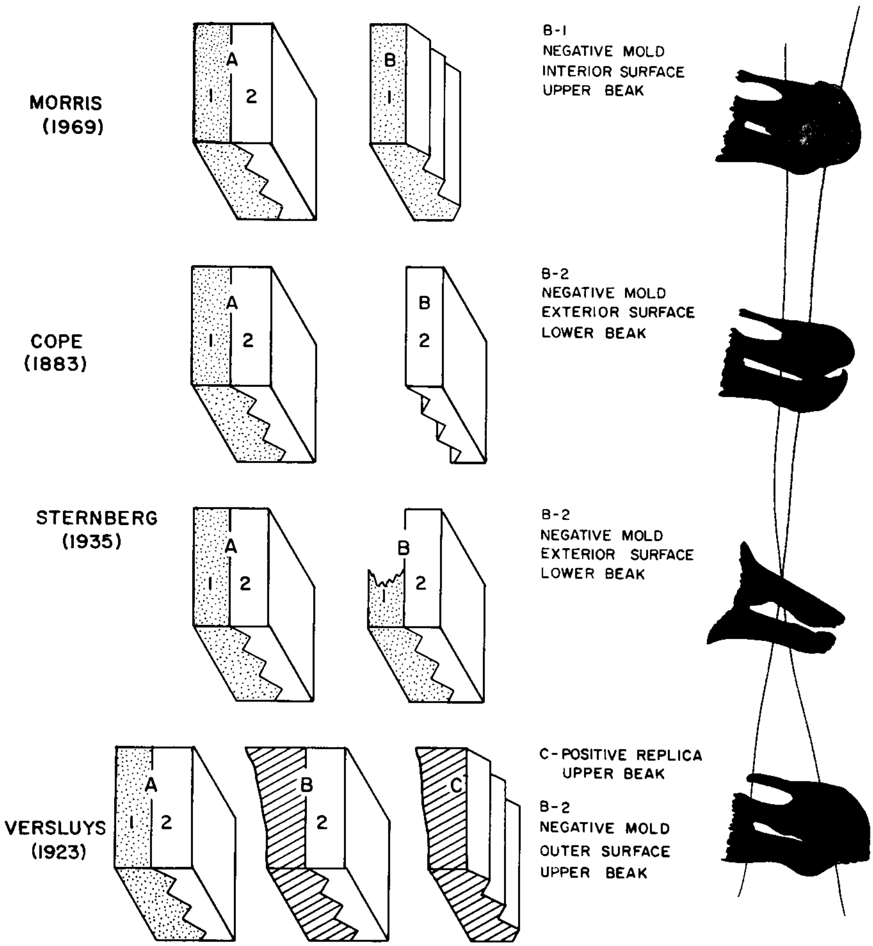

Figure 4. Diagram illustrating the interpretations of the four reported hadrosaurian bill molds. All interpretations are based upon molds preserved with specimens of *Anatosaurus annectens* except Sternberg (1935) which is based upon *Corythosaurus excavatus*. Blocks labeled represent the mold as discovered. Block 1 is the posterior part of the mold and 2 is the anterior. Blocks labeled B represent the parts of the mold preserved after preparation. Block C in the case of the interpretation by Versluys represents a plaster cast that was poured against B-2. Each group of blocks is followed by the interpretation placed upon them by the authors listed. Lastly, outline restorations are shown illustrating the interpretation by each other.

reptiles that have comparable feeding or masticating features. Cope suggested a diet of soft vegetable matter but this was based on the erroneous assumption that the teeth, in particular those of the dentary, were only loosely attached. Lull and Wright (1942:36) give the following picture, "The analogy now seems to be with the moose *Alces* whose diet is that of a browsing animal, that is the twigs and leaves of deciduous trees . . . and also certain conifers. In summer it turns to the tall, lush grass in swamps or near the margins of streams and lakes and, actually invading the water, feeds upon the leaves of the water lily or, with head entirely submerged, on the roots and stems of aquatic plants."

Versluys strongly rejected the idea of a ducklike feeding habit as reported by Abel (1912). Instead, he suggested that the structure was more beak than bill adapted for scraping bark and leaves from small scrubs and trees or even for the uprooting of plants.

There is only one report of stomach contents associated with a hadrosaurian skeleton. Unidentified plant debris and recognizable conifer needles were reported (Krausel, 1922) from the stomach cavity of *A. annectens*. As pointed out by Ostrom (1961), this might indicate merely that these creatures could feed on land plants, and it does not eliminate the possibility that they fed on aquatic vegetation as well. Indeed, the harsher fibers of land plants might be more readily preserved than the softer materials of aquatic plants.

In any analysis of their feeding habits, several morphological features must be taken into account and the assumption made that all of the features functioned together in an integrated well adapted system. The hadrosaurians were remarkably successful. Not only are their remains relatively common but genera have been recognized in North and South America and Eurasia. Despite considerable disparity, particularly in the shape of the skull, there are features related to feeding habits common to all genera. One is bulk. The probable weight of *Corythosaurus* and *Anatosaurus* was approximately 4 tons and yet the 30 to 40 foot hadrosaurians are not the largest recognized, being surpassed by *Edmontosaurus* and *Hypacrosaurus*. Small hadrosaurian remains have been collected but it is not known if these represent a truly small taxon or are immature individuals of the larger species. The few apparently undistorted skulls indicate that the hadrosaurians had a constricted buccal passage formed by the dentaries and maxillaries, and leading to the throat. In large anatosaurs, for example, it is doubtful that particles having a cross-sectional diameter larger than three or four inches could have passed along this narrow channel. Hadrosaurian dental batteries are very similar, consisting of dozens of teeth arranged in closely spaced rows. The occlusional surface is a pavement formed of the diamond-shaped crowns of the opposing dental batteries. In addition, in all genera three to six teeth are arranged in vertical rows and in each, only the most dorsal are in active use. The others serve for a highly effective replacement mechanism.

The bill as preserved in LACM 23502, seems to impose certain limiting parameters on hadrosaurian feeding habits. The structure seems best adapted for filtering. Although several workers have suggested that the bill closed

against the predentary of the lower jaw forming a cropping device, three characteristics of the bill seem to negate this function: 1) The bill was attached to the anterior and dorsal segment of the premaxillaries and its free edge extended well below the anterior dorsal margin of the predentary; 2) The very thin space between the anterior and posterior mold suggests that the bill itself was a relatively thin structure certainly not well adapted for foraging leaves and branches of trees and scrubs; 3) The last feature is the fluted, undulating inner surface of the bill which would have little or no function for foraging or browsing, and yet seems ideally suited as a filtering device.

Hadrosaurian dinosaurs, particularly such forms as *Corythosaurus* and *Hypacrosaurus*, are envisioned as mainly aquatic animals. A filtering device would be very important in assuring that these large animals could ingest large amounts of concentrated food relatively free of water in a manner similar to that of the dabbler ducks, such as *Dendrocynga, Anas* and *Aix*. These euryphagus forms have laminations on the inner surface of the dorsal bill which, when closed against the ventral bill, form an efficient filtering device. Such an interpretation certainly makes the name "duckbill" even more fitting for the hadrosaurian dinosaurs than previously supposed.

With their very efficient food gathering system, the hadrosaurs could take in all manner of food including mollusks and small crustaceans as well as plant material. In this sense they would, like many ducks, be relatively high protein as well as carbohydrate feeders. Plant material as well as more resistant invertebrates could be crushed between the broad occlusional surfaces of the impressive dental battery. By lowering the anterior part of the head, excess water as well as food particles smaller than approximately one cm would drain out of the mouth along the channels formed by the fluted bill and the opposing predentary. The resulting masticated material, highly concentrated, could then be made to flow down the very small passage between the dentaries to the stomach simply by raising the head.

The presence of the fluted bill, multiple grinding surfaces, mechanism for continuous replacement of teeth, and a constricted passage formed from the bones of the posterior mouth region makes such a feeding habit feasible.

Ostrom (1964) presents a very thorough compilation of prior hypotheses and information regarding the feeding habits of hadrosaurian dinosaurs. In his analysis of the paleoecology the conclusions reached vary only in detail from those expressed earlier (1961). In summary Ostrom states (1964:995), "Past interpretations of hadrosaurian ecology have pictured these animals as predominantly aquatic in their habits, living and feeding in swamps, lakes, or rivers and making only occasional and limited excursions out on surrounding lands. Anatomic evidence, however, contradicts this interpretation, indicating instead that the hadrosaurs as highly adept bipeds were primarily terrestrial animals. Other anatomic and botanical evidence shows them to have been active terrestrial foragers adapted for browsing on the harsher, fibrous, or even woody tissues of trees and shrubs."

The bill, as reconstructed from the mold of LACM 23502, is very thin relative to its lateral and vertical extent, and suggests a structurally weak

feature, too weak to be of use in browsing on fibrous or woody plants. Ostrom is in agreement with the conclusions presented here that hadrosaurian dental batteries together with a high degree of tooth wear must have been used to masticate food of substantial resistance; however, he suggests that this is evidence for foraging upon more resistant terrestrial vegetation. Such a dental battery could be used just as effectively for mastication of invertebrates. Ostrom (1964:987-989) suggests correctly that in the hadrosaurian localities of the Edmonton, Belly River, Judith River, Kirkland-Fruitland, Ojo Alamo and Lance marginal and aquatic vegetation are relatively rare in the paleoecosystems. This might, of course, be the result of fortuitous preservation, but even if truly representative it could be interpreted as evidence that aquatic and marginal vegetation was rare in the area where hadrosaurians were abundant, a position taken by Ostrom. On the other hand it could also be evidence for the needed addition of invertebrates in the hadrosaurian diet. One must keep in mind that the rarity of marginal and aquatic vegetation as computed by Ostrom is an absolute occurrence affected by all vagaries of preservation, but in the dynamics of the ecosystem it is the relative availability of the plants compared to the needs of the hadrosaurian that is significant.

Hadrosaurians were efficient bipeds and as Ostrom indicates (1964:990-993) the articular surfaces of the pes and hind limbs, the large fourth trochanter, ossified sacral tendons, and reduction of the carpus point strongly to this conclusion. These characteristics when treated by themselves may well suggest a terrestrial habitat but when the specialized nature of the bill is taken into consideration an alternative hypothesis seems more fitting. Therefore the conclusion that hadrosaurians were either aquatic or shallow water feeders seems appropriate. Under these circumstances the bipedalism as well as the specialized bill would be adaptively advantageous. In addition such a feeding habit would give credence to the more obvious adaptive significance of the laterally compressed tail and the probable presence of webbed hind feet, rather than to suggest that these characteristics were for protection allowing the otherwise defenseless hadrosaurian to retreat to the water when threatened (Ostrom, 1964:993-995).

RESTORATION OF HADROSAURIAN HEAD

Figures 5, A, B, and C are sketches illustrating the appearance of billed hadrosaurian dinosaurs. Evidence of bills have been found in *Anatosaurus annectens* and *Corythosaurus excavatus* but not in *C. intermedius* as restored in Figure 5C. In the skull of *C. intermedius,* however, the distal part of the dentary is greatly deflected while the maxillaries are not. The paratype skull of *C. intermedius* (ROM 4671) shows this deflection while, in the same skull, the tooth rows are occluded in normal position. If the specimen did not have a bill on the upper mandible, then there would have been a wide, opened gape at the anterior end of the mouth. The restoration of *C. intermedius* was made as this form has the most exaggerated gape of any hadrosaurian, a condition which suggests the presence of a bill, although the magnitude of the gape may be partly due to accidents of preservation.

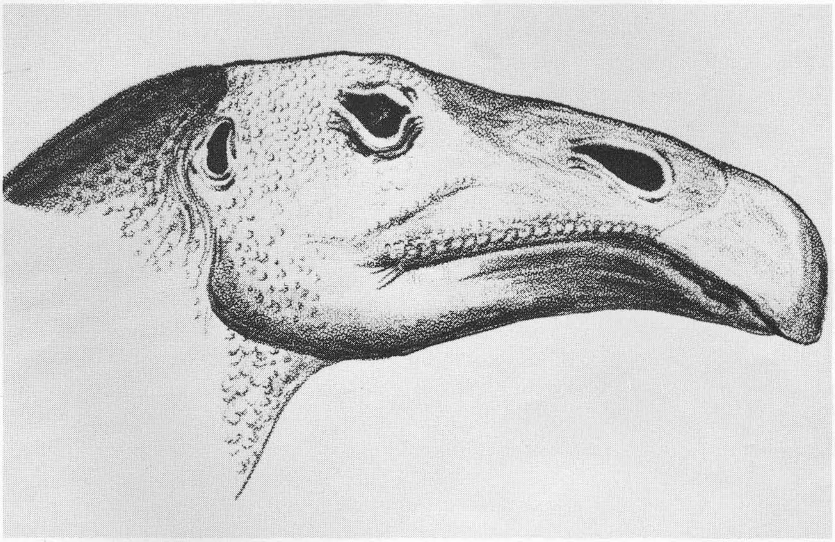

Figure 5. (A) Restoration of the skull of *Anatosaurus annectens*.

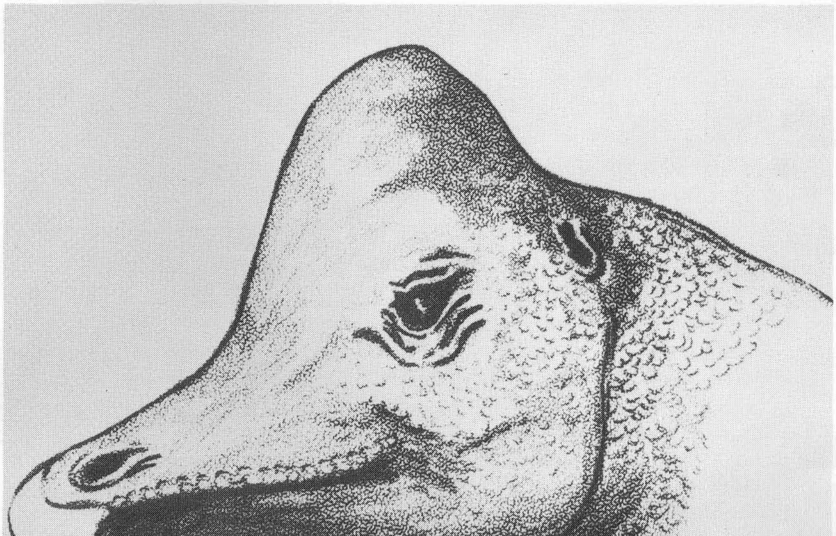

Figure 5. (B) Restoration of the skull of *Corythosaurus excavatus*.

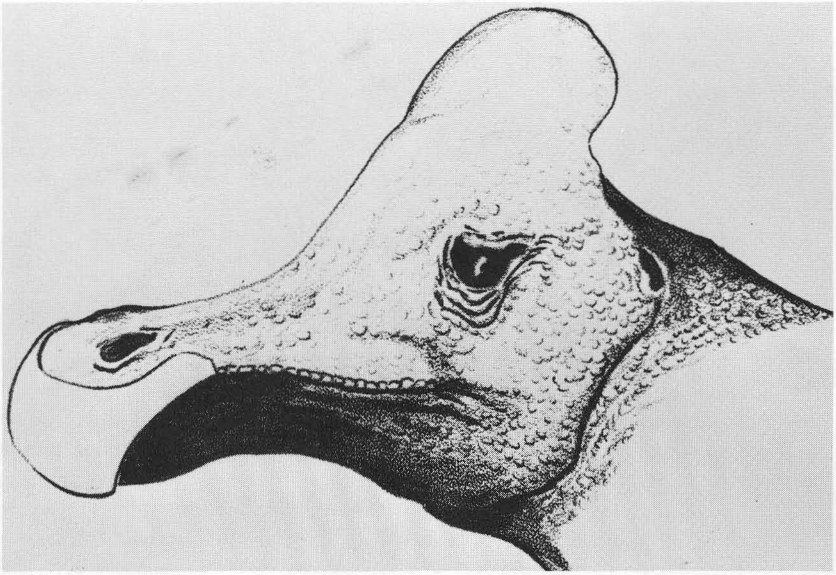

Figure 5. (C) Restoration of the skull of *Corythosaurus intermedius.*

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